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Disjunctions in the Distribution of *Eucalyptus* Species Between Western Victoria and the Mount Lofty–Flinders Ranges Area, South Australia

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Abstract: Apart from riverine and Mallee species, all eucalypts shared by Western Victoria and South Australia show range disjunctions partly related to present day low rainfall in the area between the south-east of South Australia and the Mount Lofty Ranges. All that is needed to provide habitats for continuous distributions in the past for species from coastal lowlands is higher effective rainfall or possibly lower sea-levels. It is much harder to envisage migration routes for species absent from coastal lowlands. For example, the past migration of *Eucalyptus microcarpa* to the Mount Lofty Ranges may have depended on more extensive occurrences of heavy-textured soils in the past. The disjunctions of *E. goniocalyx, E. Macrorhyncha* and *E. rubida* are even more difficult to explain as they are absent from coastal lowlands and inland plains at present. A possible migration route for the former two along ridges of Diapur Sandstone is suggested, while *E. rubida*, on which further work is needed, appears to have the most anomalous distribution of all.

INTRODUCTION

Recent distribution maps of South Australian tree species (Boomsma 1972) show many large disjunctions in the ranges of *Eucalyptus* species. A disjunction is said to occur when two populations of a species are more widely separated than its normal dispersal capacity (Cain 1944). For the eucalypts considered here, with no special adaptations for seed dispersal, seeds may be most unlikely to travel distances greater than twice tree height (Cunningham 1960). Although work is badly needed on whether occasional long distance dispersal can occur, the large number of disjunctions exceeding 100 km noted here suggest that the disjunct occurrences may be remnants of former continuous distributions and so be related to past regimes of climate and sea level. Such relationships are discussed with particular reference to the eucalypts of southern South Australia. Although most of the distribution data are readily available in Boomsma (1972), a discussion of possible past migration routes also requires detailed habitat data for the species concerned. These have been obtained from the author's field observations and from the literature. Because the eucalypts being dealt with are from sub-generic groups with centres of species diversity in Victoria and New South Wales, it is possible that migration has been mainly from these states into South Australia rather than vice versa. Nomenclature follows Boomsma (1972) except that *E. viminalis* and *E. huberana* are treated together as *E. viminalis* complex. It should be noted that Boomsma (1972) may consider *E. albens* and *E. microcarpa* together under the name *E. microcarpa*.

THE DISTRIBUTIONS

Many Mallee eucalypts show more or less continuous distributions from western Victoria to drier parts of the Mount Lofty Ranges and beyond, and riverine species like *Eucalyptus camaldulensis* and *E. largiflorens* may bridge the same area fairly completely along the Murray River (Boomsma 1972). Of the remaining eucalypts in western Victoria (i.e. those from the wetter woodland areas), not one species reaches the Mount Lofty-Flinders Ranges area without a major disjunction in its distribution. In terms of the present environment, this is probably partly correlated with the fact that only three small areas in South Australia have mean annual rainfalls exceeding 700 mm; the south-eastern extremity, a part of the Mount Lofty Ranges, and western Kangaroo Island (Fig. 1).

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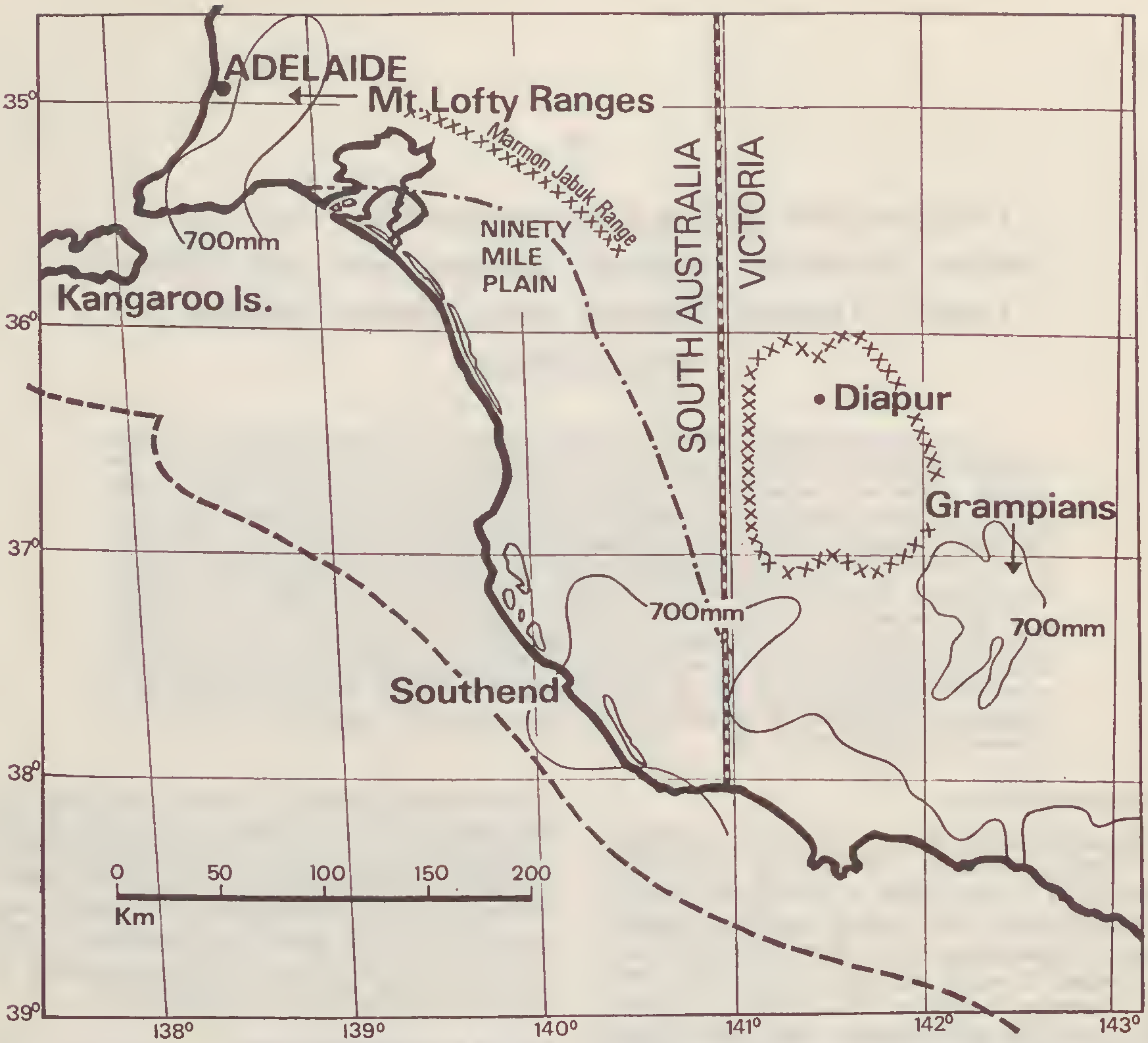

FIG. 1—The area from Western Victoria to the Mount Lofty Ranges showing place names mentioned in the text, the 700 mm mean annual rainfall isohyet, the approximate location of the southern Australian coastline during the Last Glacial (dashed line) when sea level was probably about 120 m below present, the inland margin of stranded beach ridges of aeolian calcarenite in South Australia from Blackburn, Bond and Clarke (1965) (dot and dash line) and the distribution of major areas of Diapur Sandstone, partly from Blackburn, Bond and Clarke (1967), shown by crosses. The only extensive ranges of pre-Cainozoic rocks in the whole area are the Mount Lofty and Grampians Ranges.

This leaves a dry area in and around the Ninety Mile Plain which becomes wetter towards the coast, but even there mean annual rainfall falls as low as 430 mm. This may prevent present day plant migration to and from south-western Victoria. In considering this dry coastal area as a possible past migration route it is relevant that the whole area south-east of the most inland stranded beach ridge of aeolian calcarenite (Fig. 1) is a lowland; pre-Cainozoic rocks are very rare and scattered and never form extensive ranges (Blackburn, Bond & Clarke 1965). Soils are predominantly various infertile coastal sands, shallow sandy soils on limestones, and badly drained areas of clayey and peaty soils (Northcote 1960). Fertile, well-drained medium and heavy-textured soils are very rare.

Off the present South Australian coast, Pleistocene low sea-levels more than 49 m below present are definitely known (Sprigg 1965), while world-wide eustatic sea-level changes are thought to have produced a level about 120 m below present in the Last Glacial (Jelgersma 1966). On both the coastal lowland produced by such emergence, and the coastal lowland present today, aeolian calcarenite is an important component (Sprigg 1952). It seems likely that aeolian calcarenite in the past was associated with a suite of soils similar to that now present, so that soils and topography on the Glacial lowland were probably similar to those of the present coastal area.

The disjunct eucalypts involved can be considered in four groups depending on which soils seem most likely to provide migration routes for them. Many of them occur on a wide range of other soils as well.

Species Known from Siliceous Sands

All these species (Table 1) are common in coastal and sub-coastal areas on siliceous sands, in the case of *E. ovata* (Fig. 2) usually on peaty horizons over sand around swamp margins. All occur in the south-east of South Australia, and to provide a past migration corridor to the Mount Lofty Ranges, all that is required is an increase in effective rainfall with the sea at its present level.

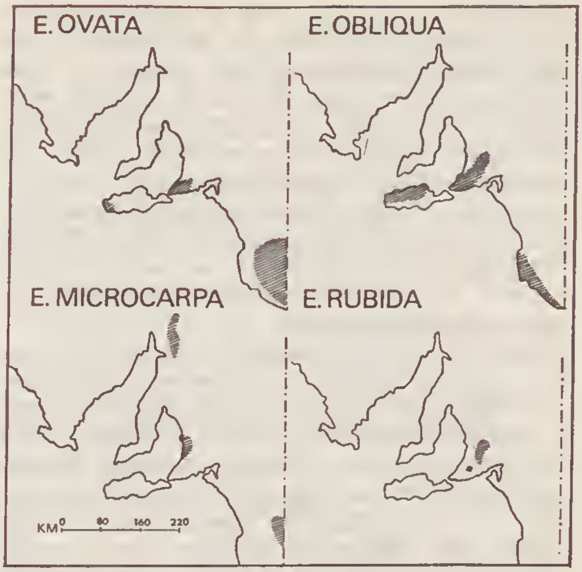

Fig. 2—Distribution of four species of *Eucalyptus* in South Australia from Boomsma (1972).

Table 1

DISTRIBUTION AND HABITAT DATA FOR WESTERN VICTORIAN *Eucalyptus* SPECIES WITH DISJUNCT OCCURRENCES IN SOUTH AUSTRALIA, AFTER BOOMSMA (1972)

	Approximate lower rainfall limit in South Australia (as mean annual rainfall in mm)	Ocurrence in South Australia					
		Lower south-east	Upper south-east	Mount Lofty Ranges	Flinders Ranges	Kangaroo Island	References*
Species known from Siliceous Sands							
E. baxteri	460	X	X	X		X	Litchfield (1956)
E. fasciculosa	460	X	X	X		X	White (1970)
E. obliqua	610	X		X		X	
E. ovata	610	X		X		X	
E. viminalis complex	460	X	X	X		X	Litchfield (1956)
Species known from Aeolian Calcarenite							
E. leucoxylon	460	X	X	X	X	X	Litchfield (1956)
Species known from Medium and Heavy-textured Soils							
E. microcarpa	480		X	X	X		
Species known from Ranges of pre-Cainozoic Rock							
E. goniocalyx	580			X	X		
E. macrorhyncha	610				X		
E. rubida	760			X			

* *In addition to Boomsma* (1972)

Alternatively a Glacial drop in sea-level would expose country south-east of the present coast which would probably be wet enough to allow continuous distribution if rainfall regimes were the same as at present (see also Parsons 1969). This assumes that suitable soils were present on the Glacial coastal lowland, which seems likely.

Another disjunct species in this category for which similar explanations could apply is *Banksia marginata* (Boomsma 1972), as well, probably, as other sclerophyllous species with similar climatic and edaphic ranges.

Western Victorian species in this 'coastal-siliceous' category include *E. kitsoniana* which does not reach South Australia, and *E. vitrea** and *E. pauciflora* (as well as *Acacia mearnsii*) which reach the south-east of South Australia, but do not occur anywhere else in the state (Boomsma 1972). The reasons for these restricted distributions are enigmatic; perhaps these species reached western Victoria at a time when migration routes to the Mount Lofty Ranges were no longer available.

Species Known from Aeolian Calcarenite

The one species in this group, *E. leucoxylon*, is rare on siliceous sands, but occurs on shallow soils on Pleistocene aeolian calcarenite, for example at Southend in South Australia (Fig. 1). The distribution of such soils (Northcote 1960) could easily provide a coastal migration corridor. under the same conditions as those specified for the previous group (some of which also occur on aeolian calcarenite).

Species Known from Medium and Heavy-textured Soils

E. microcarpa (Fig. 2) appears closely restricted to relatively fertile, well-drained medium and heavy-textured soils, and in keeping with this is absent from the south-east extremity of South Australia and all of the coast from there to the mouth of the Murray River. As soils near the present coast and possibly also of the Last Glacial coastal lowland seem unlikely migration routes, an alternative route may be necessary.

A more direct route linking the present occurrences near Bordertown in the upper south-east of South Australia with those near Adelaide would be along a straight line linking these two places, but this seems to be at least partly closed by sandy infertile soils in the Ninety Mile Plain.

* The type of *E. vitrea* R. T. Baker is considered by others to be a hybrid; if so the name could not be applied to this species (see Pryor, L. D. and Johnson, L. A. S., 1971. *A classification of the eucalypts*. Australian National University, Canberra).

The present occurrences near Bordertown are on cracking clay soils thought to indicate a former location of alluvial tracts on the Murray Basin plain (Blackburn 1962a). Extensive areas of deep heavy clays are known beneath the present land surface inland from the inland margin of aeolian calcarenite in the Ninety Mile Plain (Fig. 1) and these areas may also be related to former alluvial tracts on the Murray Basin plain (Litchfield 1956). It would be most interesting to know the former extent of surface clay in this area to see if it could have provided a suitable migration route for *E. microcarpa*.

Two species showing disjunctions according to Boomsma (1972), and which are possibly in this group, are *E. odorata* and *E. porosa*. These are omitted here, as difficulty in separating them means that their edaphic ranges are badly known and as Boomsma's (1972) maps do not appear to include all the records of them by Litchfield (1956). Taken together, these two closely related species may extend almost continuously from Bordertown to the Mount Lofty Ranges through the Ninety Mile Plain (Boomsma 1972, Litchfield 1956).

Species Known from Ranges of Pre-Cainozoic Rock:

E. goniocalyx is fairly closely restricted to slopes and foothills of Flinders, Mount Lofty and Great Dividing Ranges, usually on shallow, rocky or gravelly soils. Of the coastal records in Hall, Johnston and Chippendale (1970), some are on hillslopes of pre-Cainozoic rocks (e.g. near Melbourne) and others are likely to be errors (see Boomsma 1972, Parsons & Kirkpatrick 1972). As *E. goniocalyx* has not been recorded from coastal sands or any other coastal or near-coastal lowland soils in areas where climate is suitable for it, it is hard to envisage a continuous migration route near to the present coast or seaward from it in times of low sea level. The species is unknown from inland plains, so these are also unlikely migration routes. The most plausible migration route on pre-Cainozoic rocks would appear to be along the granite of the Padthaway Ridge in the Ninety Mile Plain area (Parkin 1969) at some stage in the Cainozoic. Although granite outcrops are very small and very scattered at present (Blackburn, Bond & Clarke 1965), they could have been more or less continuous from Pliocene to early Pleistocene times until much of the Ridge was probably submerged later in the Pleistocene (J. B. Firman pers. comm.). To provide a more recent continuous migration route on ranges of pre-Cainozoic rocks, species would have to migrate north up the Great Dividing

Range to Queensland and then follow the Gray and Barrier Ranges down to the Flinders Ranges.

However, there is an interesting exception to the general occurrence of *E. goniocalyx* on soils on pre-Cainozoic rocks. At its western limit in Victoria (Blackburn 1963) the species extends beyond ranges of such rocks, but only onto ridges of Diapur Sandstone (Blackburn pers. comm.), which is thought to be of Pliocene age (Brown, Campbell & Crook 1968). Soils on these ridges resemble those carrying *E. goniocalyx* on ranges of pre-Cainozoic rocks in their acidic topsoils; in the rocky, gravelly character imparted by their ironstone gravel and sandstone; and in their elevated position above the surrounding plains.

These ridges of Diapur Sandstone (equivalent to Parilla Sand) are thought to represent beach dunes stranded during the Pliocene retreat of the sea (Brown, Campbell & Crook 1968). To the west, very similar sandstone interpreted as equivalent to Diapur Sandstone occurs in the Marmon-Jabuk Range (Fig. 1) where it is buried by later sediments (Jessup & Wright 1971). Although this range is not at present continuous with the areas of Diapur Sandstone in Victoria, there is some Diapur Sandstone in the intervening area north of Bordertown (Blackburn 1962). If ridges of the sandstone do represent coastlines of the former Murravian Gulf (Jessup & Wright 1971), it is possible that they were formerly more or less continuous from near the Grampians almost to the Mount Lofty Ranges, so that they may constitute a possible migration route for *E. goniocalyx*. If such migration did occur, this would certainly imply a previous climate of higher effective rainfall than at present.

E. macrorhyncha has a very similar edaphic range to *E. goniocalyx* (with which it often cohabits), being both fairly closely restricted to pre-Cainozoic rocks, and absent from coastal lowlands or inland plains. Although it is not known from soils on Diapur Sandstone, it is known from very similar ironstone-rich soils on Tertiary deposits, as in the Brisbane Ranges near Melbourne. If a relatively continuous migration route has to be chosen on the basis of its present day ecological tolerances, again ridges of Diapur Sandstone may be more likely than the other routes available.

E. rubida (Fig. 2) is ecologically similar to the previous two species, but with a wetter lower rainfall limit (Table 1). Although often found on deeper soils than are *E. goniocalyx* and *E. macrorhyncha*, it is again absent from coastal lowlands and inland plains. Like *E. macrorhyncha* it appears to reach its western limit in Victoria in the Grampians area. It is not known from soils on Diapur Sandstone or from similar soils and may more strongly suggest past migration on soils on pre-Cainzoic rocks like those of the Padthaway Ridge than the other species. In any case, past migration to the Mount Lofty ranges implies a previous effective rainfall higher than that necessary for migration of any other species considered (Table 1). Also, *E. rubida* extends to colder sites in the eastern states than *E. goniocalyx* and *E. macrorhyncha*, but whether this is significant for any past migrations is not known.

It is also of interest that many of the associates of *E. goniocalyx, E. macrorhyncha* and *E. rubida* on pre-Cainozoic ranges in Victoria, such as *E. dives, E. polyanthemos, E. radiata* and *E. sideroxylon* do not occur in South Australia. The reasons why *E. rubida*, for example, should occur in the Mount Lofty Ranges, but not these other species, are completely obscure.

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